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Biogeographic Patterns of Iranian Lepidoptera: A Framework for Conservation

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ABSTRACT

Aim: The contact zone of three zoogeographic realms, the Palearctic, Saharo-Arabian and Oriental, is an evolutionary cradle of high species richness and endemism in Iran. In this study, we investigate statistically inferred bioregions of Lepidoptera in this region. Additionally, we assess species turnover and potential conservation gaps across the defined bioregions in this country.

Location: Iran.

Taxa: Lepidoptera.

Methods: Potential ranges of Lepidopteran species were estimated using species distribution modelling and masking unsuitable ecosystem patches within a Minimum Convex Polygon, utilising the most comprehensive dataset available for the group to address the knowledge gaps in their known distribution. A presence/absence matrix was generated to define bioregions using clustering- and network-based methods. We then assessed the faunistic relationships of the defined bioregions and the degree of coverage of these regions by the network of protected areas (PAs) within the country.

Results: Despite some differences, the presence of five main bioregions for Lepidoptera was suggested by both clustering- and network-based methods. Beyond this, six and seven small zones were detected respectively, on the overlapping areas of major bioregions as potential transition zones. Ultimately, we found an uneven distribution and extensive gap of PAs across the detected bioregions.

Main Conclusions: The results of this study suggest a crucial transitional position of Iran between three main global zoogeographic realms. While similar to the results of the clustering-based method, the bioregions detected by the network-based method are more compatible with previously identified ecoregions, macrobioclimates and phytogeographical regions of the country. The most diverse defined bioregions and transition zones in this study are on average protected by less than 10% of their total areas. Further studies are needed to investigate the historical and ecological drivers that differentiate the species assemblages between bioregions and zoogeographic realms.

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1 | Introduction

Biogeographic regions are distinct spatial units of species co-occurrence, subdividing biomes into meaningful clusters of exclusive species assemblages (Olson et al. 2001; Carstensen et al. 2013; Antonelli 2017; Edler et al. 2017; Ficetola et al. 2017; Woolley et al. 2020). These units provide a framework for understanding the historical evolution of habitats with their biological communities and associated environmental drivers (Carstensen et al. 2013; Antonelli 2017; Ficetola et al. 2017). Hence, the concept of biogeographic regions plays an important role both in fundamental studies of biogeography and evolution and in practical studies, for which biodiversity conservation is a prime example (Olson et al. 2001; Kreft and Jetz 2010; Bloomfield et al. 2018; Montalvo-Mancheno et al. 2020; Woolley et al. 2020).

While early works on bioregionalization were mainly expert-based (Sclater 1858; Wallace 1876; Elton 1946), various statistical approaches have later been developed to define distinct bioregions based on quantifiable criteria, e.g., species (dis)similarity (Kreft and Jetz 2010; Carstensen et al. 2013; Vilhena and Antonelli 2015). The two main approaches currently used are clustering-based (CM) and network-based (NM) methods (Carstensen et al. 2013; Bloomfield et al. 2018; Edler et al. 2017). While CM clusters bioregions according to the distance between the sites (e.g., grid cells) based on the (dis)similarity of contributed species in each site (Bloomfield et al. 2018), NM, using the *infomap* algorithm, considers the correlation between species occurrence and sites (as two-mode or bipartite network), and consequently, this method is able to identify and group together species and sites that are strongly interconnected (Carstensen et al. 2013; Vilhena and Antonelli 2015; Edler et al. 2017). *Infomap* is one of the network-based algorithms, which aims to efficiently find the optimal community structure in a large-scale network based on the *Map equation* (Edler et al. 2017). The Map equation method shows a better performance for detecting small bioregions and interzones (Bloomfield et al. 2018). A comparison of the bioregionalizations as estimated using both methods may help to define bioregion more objectively.

Transition zones are located where bioregions overlap along with shifts in biotic (species composition) and abiotic features (climate, geology, etc.; Morrone 2004; Ferro and Morrone 2014). These regions are characterised by complex species assemblages with different affinities (Halffter and Morrone 2017; Morrone 2023), which are the result of evolutionary and ecological differentiation (Halffter and Morrone 2017; Morrone 2023). Iran is located at the meeting point of three global zoogeographic realms for vertebrates (Palearctic, Saharo-Arabian and Oriental; Holt et al. 2013; Ficetola et al. 2017; Figure 1). The country is characterised by high landscape heterogeneity on the one hand and steep climatic gradients on the other, which leads to a high habitat diversity and heterogeneity (Figure 1). Landscape complexity and climate heterogeneity are reflected in the species composition of the fauna and flora (Noroozi et al. 2018; Rajaei, Noori, et al. 2023; Yusefi et al. 2019; Yousefi et al. 2023), highlighting the importance of the country as a macro-scaled transition zone between different regions with outstanding biodiversity (Yusefi et al. 2019; Yousefi et al. 2023). However, there is a significant deficiency in our knowledge of biodiversity and distribution patterns of the majority of faunal groups in Iran.

Despite the high biodiversity and endemism of the country (Noroozi et al. 2018; Rajaei, Noori, et al. 2023), there are only a few studies investigating the biogeography of the species composition, particularly for invertebrates (Dubatolov and Zahiri 2005; Matov et al. 2008; Paknia and Pfeiffer 2011). Phytogeographical studies consistently subdivided Iran into regions compatible with macro-bioclimatic regions (White and Léonard, 1991; Djamali et al. 2011). On the other hand, zoogeographic studies mainly focused on well-known species of vertebrates such as mammals (Blanford 1876; Yusefi et al. 2019), birds (Zarudny 1911; Scott et al. 1975), reptiles (Anderson 1968) and fishes (Coad 1985), which revealed different numbers of bioregions based on the studied groups. These studies suggested different affiliations for species assemblages to various zoogeographic regions, particularly in the southern parts of the country. Furthermore, previous studies revealed a large conservation gap even for vertebrates and plants (Farashi et al. 2017; Noroozi et al. 2018; Noroozi et al. 2019; Yusefi et al. 2019; Noori et al. 2021; Yousefi et al. 2023) and lepidopterans in Iran (Noori, Rödder, et al. 2024).

Nevertheless, additional studies based on larger datasets may provide a better portrait of the faunal complexity at overlaps between bioregions. To do so, we here investigate the bioregionalisation of the recently catalogued order Lepidoptera in Iran (Rajaei, Aarvik, et al. 2023), as one of the most diverse and species-rich insect groups with at least 4812 confirmed species (Rajaei, Noori, et al. 2023) and over 9000 species estimated for the country (Landry et al. 2023). Additionally, we filled the gaps in the known distribution of the studied Lepidoptera species using a predictive modelling approach.

In this study, we aim (1) to delineate bioregions within Iran based on the three best-studied Lepidoptera families (Geometridae, Lycaenidae and Zygaenidae) and evaluate the differences with previous regionalization studies. Apart from a well-known taxonomy, each of these three families has a distinct biology, ecology, behaviour and adaptation, likely increasing the robustness of our results; (2) to investigate the distribution of the most diverse regions for Lepidoptera; (3) to assess the spatial overlap between the network of protected areas across bioregions for Lepidoptera; and finally (4) to investigate the species turnover within the transition zones between different major bioregions and zoogeographic regions.

2 | Material and Methods

2.1 | Occurrence Dataset

In this study, we used the most comprehensive set of occurrence data for Iranian Lepidoptera (Rajaei, Aarvik et al. 2023; See Appendix S1). As the taxonomy and distribution patterns of most lepidoptera families in Iran are only fragmentarily understood (Landry et al. 2023), we focused only on three families (namely, Geometridae, Lycaenidae, Zygaenidae) based on the following three criteria: (i) they are taxonomically well-studied

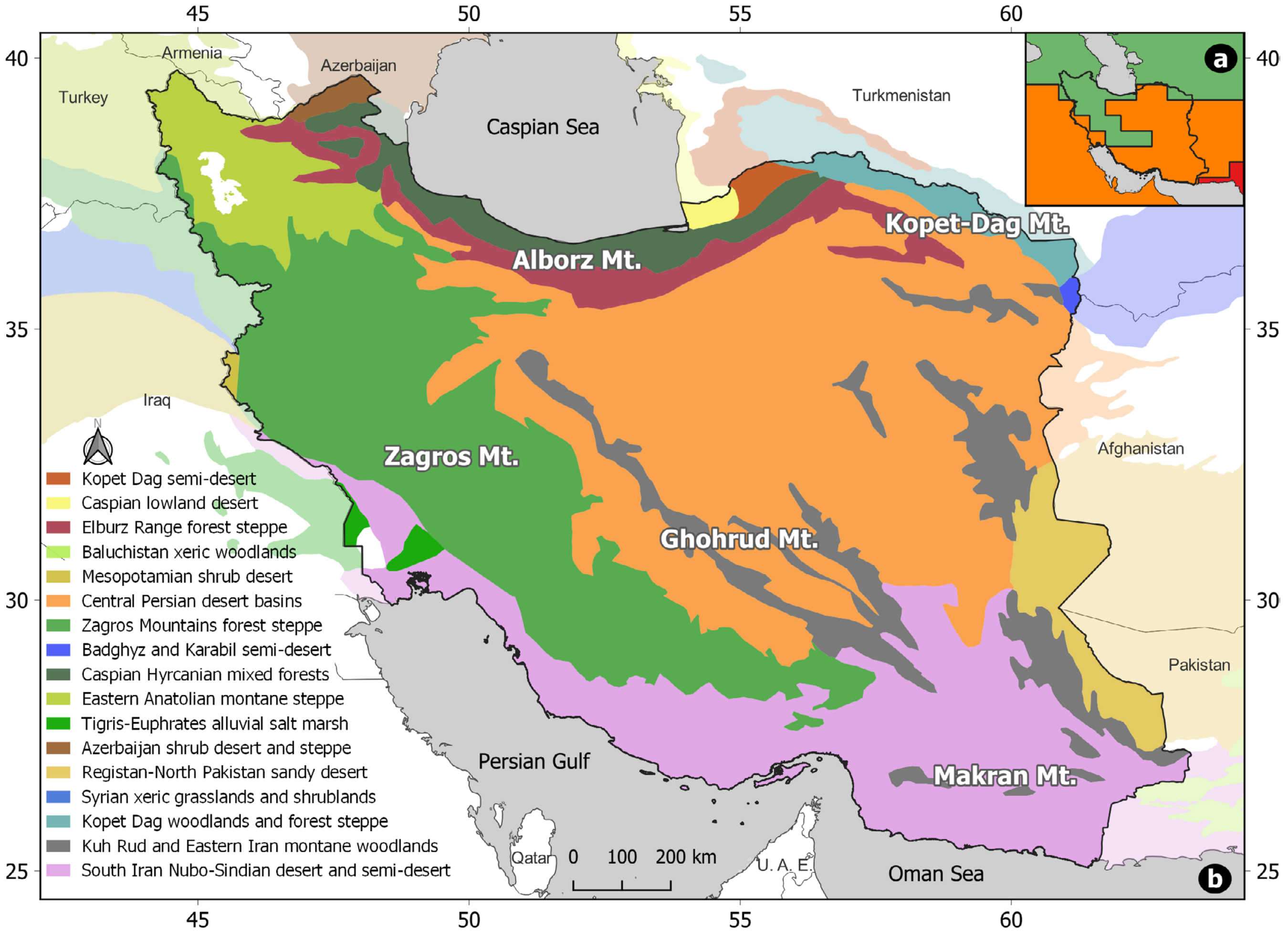

FIGURE 1 | (a) The map depicts the location of Iran in the southwest of Asia at the intersection of three zoogeographic realms for vertebrates: Palearctic (green), Saharo-Arabian (orange) and Oriental (red); after Holt et al. 2013. (b) A modification for identified ecoregions for the study area and neighbouring countries by Dinerstein et al. (2017), and the names of five main mountain ranges.

TABLE 1 | Structure of the dataset for selected families of the Lepidoptera in Iran. Min stands for minimum number of occurrences per species in the dataset, and Max depicts the maximum number of occurrences. Endemism shows the percentage of endemic species for each family.

		Number of records				
Family	**Number of species**	**Records**	**Min**	**Mean**	**Max**	**Endemism**
Lycaenidae	209	8587	1	41	532	28%
Geometridae	515	5279	1	10	164	21%
Zygaenidae	73	1164	1	16	68	50%

in the country; (ii) they have a high number of species with occurrence data; (iii) they have distinct ecology, biology and distribution patterns in each family.

The family Lycaenidae (gossamer-winged butterflies) with 215 species is the largest family in the super-family of Rhopalocera (butterflies) in Iran (Nazari 2003; Tshikolovets et al. 2014). Geometridae (geometer moths), with 539 species, is the best known family within the clade of Macroheterocera (moths) in the country (e.g., Rajaei 2012; Rajaei et al. 2012, 2013; Rajaei, Hausmann, Trusch et al. 2022; Rajaei, Aarvik, et al. 2023; Wanke, Hausmann, Krogmann et al. 2020; Wanke et al. 2019; Wanke, Hausmann, Sihvonen, et al. 2020), and Zygaenidae (burnet moths) has 73 species and an extremely high rate of endemism (46%) (e.g., Naumann et al. 1999; Keil 2014; Hofmann and Tremewan 2017, 2020a, 2020b; Rajaei, Aarvik, et al. 2023). While Geometridae are nocturnal, Lycaenidae and Zygaenidae are active during the day (Hausmann 2001; Hofmann and Tremewan 2017). We gathered occurrences for 209 species of Lycaenidae, 515 species of Geometridae and 73 species of Zygaenidae in the final dataset (Table 1; Figures S1 and S2).

Generating potential species range Defining species ranges has been commonly used to overcome data deficiencies and bias in sampling efforts, which can result in overestimating the species distribution (Woolley et al. 2020; Ginal et al. 2022; Hughes et al. 2024). Considering that there has not been any systematic survey of any Lepidoptera species in Iran, we carefully generated a potential distribution range for each species to overcome the potential biases and fill the knowledge gaps in their known distribution (van Proosdij et al. 2016; Woolley et al. 2020; Hughes et al. 2024). Many species, particularly the endemic ones, were represented in the dataset with few or even single records (Appendix S1; Figures S1 and S2). Therefore, we applied different strategies based on the number of occurrences to estimate the species ranges (Doré et al. 2022). For a better comparison, three different approaches were employed to define the presence/absence of the studied species based on (i) only occurrences, (ii) a Minimum Convex Polygon with masking unsuitable ecosystems (MCP) and (iii) a combination of MCP and species distribution models (MCP + SDM; a detailed description of each approach can be found in Appendix S1). To summarise the presence/absence and frequency of each species was estimated across a grid with a size of 0.5° (55 × 55 km) within the study area, to be then converted into a presence/absence matrix (PAMatrix) for bioregionalization analysis (Figure S3). To generate this PAMatrix using occurrences only, we converted the occurrences to a raster file at a resolution of 1 km and then scaled it up to 0.5° (Appendix S1). For generating MCP, first we generated a MCP polygon based on species occurrences and then narrowed down the polygon area by masking unsuitable ecosystem patches within the Terrestrial Ecosystem Map patches (TEM; Sayre et al. 2020) at 1 km. Finally, in the MCP + SDM approach, we generated species ranges using a combination of MCP and species distribution models (SDMs) to define suitable areas for the species.

To define potential species ranges, we created a dispersal mask using MCP + SDM, narrowing the MCP area to suitable ecosystem patches (Sayre et al. 2020). This mask was applied to delimit the final ensembled SDMs. To model the distribution of the species, we used the Maximum Entropy (*MaxEnt*) algorithm using the *raster* and *terra* package in R following Ginal et al. (2022). Several models were fitted for each species and finally those models with the highest performance were used to ensemble the final model across various replicates (Ginal et al. 2022; Noori, Rödder, et al. 2024; for a detailed workflow see Appendix S1 and Data S1). Finally, the resulting PAMatrix from the abovementioned approaches were the basis for bioregionalization methods to cluster species assemblages (Figure S3).

2.2 | Bioregionalization

The bioregionalization analyses were conducted for all families together and separately for each family (see Data S2). We concatenated the resulting PAMatrix for all studied families to generate a master PAMatrix for the bioregionalization analyses (Figure S3).

2.2.1 | Clustering-Based Bioregionalization

To cluster the grid cells (cells) of the study area, we generated a distance matrix based on the PAMatrix using the *bioregion* package (Denelle et al. 2025) in R. We used Simpson's dissimilarity between species assemblages of cells to determine the clusters (Kreft and Jetz 2010). This metric is less sensitive to richness differences between the study units, which is useful for studying the compositional differences in species assemblages (Baselga 2010; Kreft and Jetz 2010; Leprieur and Oikonomou 2014; Castro-Insua et al. 2018). To find the optimal number of clusters, we generated hierarchical trees with different cut-offs (2 to 30) and simulated the clustering by randomising the order of sites within the distance matrix for 100 trials (Denelle et al. 2025). Then, the optimum partitioning of the tree was evaluated using the *partition_metrics* function using the *pc_distance* method (Holt et al. 2013; Denelle et al. 2025). We followed Edler et al.'s (2017) approach to define indicative and common species for CM (Table 2). Using species presence frequencies in 0.5° cells, we calculated a score reflecting the likelihood of finding a species in a bioregion relative to others. Species with the highest scores (> 20%) were deemed indicative, while those with the lowest were classified as common species (Table 2).

2.2.2 | Network-Based Bioregionalization

We clustered the distribution of the species using network-based community detection algorithms (*infomap*) embedded in the online interactive approach of *Infomap bioregion* (v. 2; Vilhena and Antonelli 2015; Edler et al. 2017). We used occurrences generated from the potential species ranges generated by different approaches in *Infomap bioregion* (Edler et al. 2017). Based on the resulting occurrence of the ranges, a bipartite network was generated between the species' occurrences and the cells of the study area. This network was then clustered into a set of bioregions based on species assemblages. The *Infomap bioregions* application also reports the common and indicative species of each bioregion as defined above for CM. We used this application due to its higher handling efficiency and more easily interpretable results (Edler et al. 2017). The application was tuned as follows: the size of the grid cells was considered as 0.5° to be comparable with the results of the CM (see Appendix S1). Since some species in our dataset occurred only in very small areas, we considered a minimum cell capacity of 1 and a maximum of 300 to make it comparable to the results of the CM. Following Edler et al. (2017), we used 100 trials with default values for other parameters (e.g., Markov time) to reach an optimal consensus of the number of detected bioregions.

2.3 | Conservation of Bioregions

Finally, we assessed the overlap between the network of the protected areas (PAs) in Iran with the extent of the detected different bioregions by NM and CM based on the MCP + SDM approach (Table 3). We used the last updated polygons of the PAs within the country (Iranian Department of Environment, 2023: https://en.doe.ir/). Overall, our dataset contains 378 PAs in five IUCN categories (National parks, Wildlife refugia, Natural monuments, Protected areas and Protected rivers), which roughly cover 11% of the country's area (Noori, Rödder,

TABLE 2 | A comparison of bioregionalization results by clustering-based (CM), and network-based (NM) methods.

Bioregion/ transition zone	Detected bioregions		Most indicative species	
	CM	NM	CM	NM
Alborz	5	1, 2, 8	*Polyommatus erotulus*, *P. zapvadi*, *Lycaena virgaureae* $^{\text{Lyc}}$; *Lithostege witzenmanni*, *Stegania dilectaria*, ***Lithostege stadiei*** $^{\text{Geo}}$; ***Zygaena christa***, ***Z. tenhagenova***, ***Z. mana*** $^{\text{Zyg}}$	***Polyommatus peilei***, *P. marcid*, *P. Iuna*, *P. myrrhinus* $^{\text{Lyc}}$; *Lithostege witzenmanni*, ***Scotopteryx decolor, Idaea wiltshirei*** $^{\text{Geo}}$
Zagros	1, 5	1, 8	***Polyommatus Zarathustra***, ***Neolysandra fereiduna***, ***P. shahrami*** $^{\text{Lyc}}$; ***Euphyia farsica***, ***Dicrognophos culminate***, *Kresnaia beschkovi* $^{\text{Geo}}$; ***Rhagades tarmanni***, ***Z. naumanni***, ***Jordanita christinae*** $^{\text{Zyg}}$	***Polyommatus peilei***, *P. antidolus*, *P. Iuna* $^{\text{Lyc}}$; ***Idaea wiltshirei***, *Kresnaia beschkovi* $^{\text{Geo}}$; ***Zygaena mirzayansi, Z. naumanni*** $^{\text{Zyg}}$
Central desert basins	2	3	***Plebejus ardashir***, ***Polyommatus eckweileri***, ***P. pseudoxerxes*** $^{\text{Lyc}}$; *Hydrelia chionata*, *Eupithecia gueneata*, *Idaea deversaria* $^{\text{Geo}}$; ***Zygaena fusca***, ***Zygaenoprocris efetovi***, ***Z. hofmanni*** $^{\text{Zyg}}$	***Polyommatus baltazardi***, ***Plebejus ardashir***, ***P. kermansis*** $^{\text{Lyc}}$; ***Rhodostrophia vahabzadehi***, ***Nychiodes mirzayansi*** $^{\text{Geo}}$; ***Zygaenoprocris hasarani***, ***Zygaena aisha*** $^{\text{Zyg}}$
Persian Gulf and the Oman Sea coasts	3	4	*Azanus ubaldus*, ***Polyommatus sephidarensis***, $^{\text{Lyc}}$; ***Scopula gracilis***, *Hyperythra swinhoei*, ***Nebula saidabadi*** $^{\text{Geo}}$; ***Zygaenoprocris duskei*** $^{\text{Zyg}}$	*Azanus ubaldus*, *Anthene amarah* $^{\text{Lyc}}$; ***Scopula lactarioides***, *Isturgia disputaria*, *Microloxia indecretata*, *Pseudosterrha paulula*, *Zamarada minimaria*, *Idaea mimetes*, *Gonodontis clelia* $^{\text{Geo}}$
Kopet-Dag	4, 6, 7	5, 7	*Polyommatus dorylas*, ***P. tenhageni***, *P. phyllides* $^{\text{Lyc}}$; ***Scotopteryx kurmanjiana***, *Eupithecia turkmena*, *Digrammia rippertaria* $^{\text{Geo}}$; ***Zygaenoprocris khorassana***, ***Z. fredi***, *Z. minna* $^{\text{Zyg}}$	*Polyommatus tenhageni*, *Neolycaena tengstroemi*, *Turanana dushak* $^{\text{Lyc}}$; *Cinglis eurata*, *Protorhoe turkmenaria*, *Stegania dalmataria* $^{\text{Geo}}$; ***Zygaenoprocris khorassana***, ***Z. fredi***, ***Zygaena esseni*** $^{\text{Zyg}}$
Central Zagros	1, 2, 3	6	*Scopula hoerhammeri*, *Idaea wiltshirei*, *Eupithecia mahomedana*, ***E. brandti***, *E. sectile*, *E. cheituna*, *E. aduncata*, *E. bastelbergeri*, *Eumera hoeferi* $^{\text{Geo}}$	
Khuzestan plain	1, 3	10	*Phaiogramma polemia*, *Isturgia hopfferaria*, *Scopula relictata*, *Eupithecia ultimaria*, ***Pasiphila palaearctica***, *Dicrognophos sartata* $^{\text{Geo}}$	

Note: The table includes the suggested names for the five detected bioregions and transition zones, followed by the corresponding region IDs by each method, and a list of the most indicative species for each bioregion in different families of Lepidoptera: Lycaenidae (Lcy), Geometridae (Geo) and Zygaenidae (Zyg). The endemic species are shown in bold.

TABLE 3 | The coverage of the network of the protected areas (PAs) across bioregions of Lepidoptera detected by network-based method in Iran.

Bioregion name	Area of bioregion (km^2)	Number of protected areas	Protected areas (km^2)	% Protected
1 (Zagros)	331,878 (20.1%)	90	31,454	9.5
2 (Alborz)	155,717 (9.45%)	77	20,296	13.0
3 (Central desert Basins)	661,255 (40.1%)	54	96,533	14.6
4 (Persian Gulf)	309,892 (18.8%)	41	20,571	6.6
5 (Kopet-Dagh)	89,329 (5.42%)	24	6626	7.4
6 (Central Zagros)	22,160 (1.34%)	8	2064	9.2
7 (Northeast)	5056 (0.3%)	6	697	13.8
8 (Northwest)	18,819 (1.14%)	1	1428	7.6
9 (Taftan)	10,738 (0.65%)	2	3.26	0.03
10 (Khuzestan)	15,338 (0.93%)	6	2794	18.2
11 (Makran)	4752 (0.28%)	0	0	0

Note: The table includes information about the area and percentage of the country's land, number and areas of PAs, and the coverage percentage of PAs across each bioregion and transition zone.

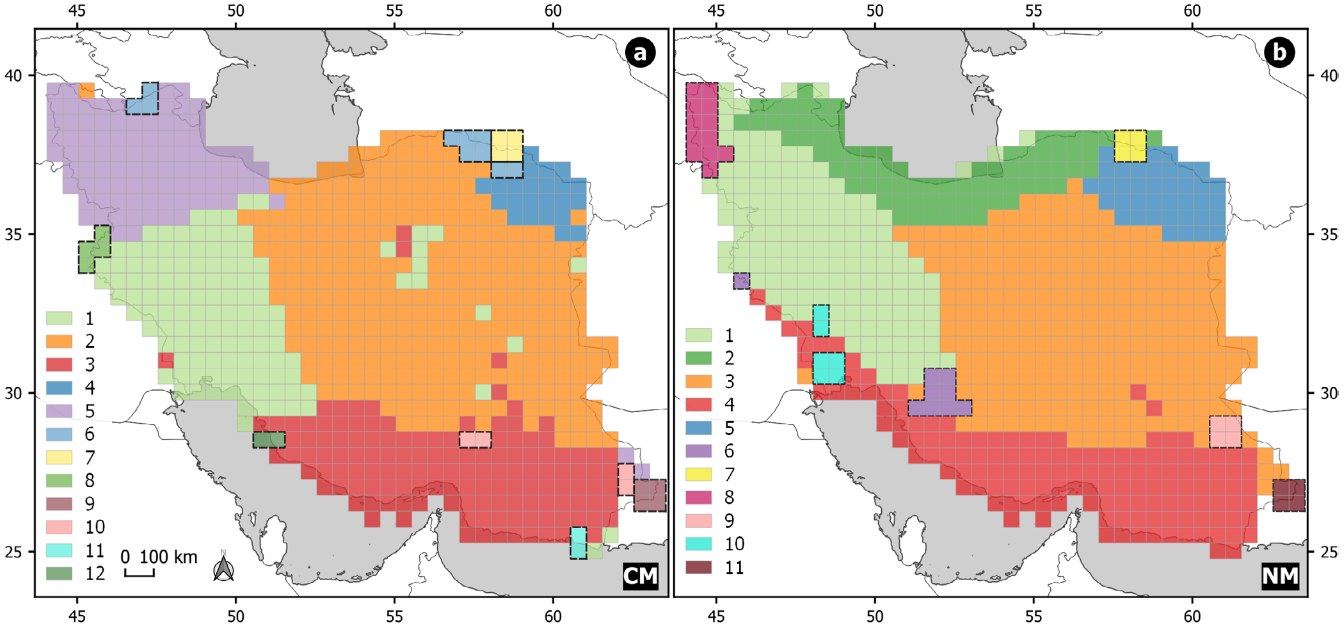

FIGURE 2 | Bioregionalization of Iranian Lepidoptera based on the three families of Lycaenidae, Geometridae and Zygaenidae using (a) clustering-based (CM) and (b) network-based methods (NM). The potential transition zones have been highlighted by dashed lines.

et al. 2024; Noori, Zahiri, et al. 2024). We calculated the area of coverage and the number of PAs to represent the rate of conservation for each detected bioregion.

3 | Results

The results of this study show some convergence between the number of detected geographic units using clustering-based (CM, with 12 units) and network-based methods (NM, with 11 units). Disregarding small regions (with less than 12 cells), both methods yielded five main geographic units (hereafter bioregions) for the Lepidoptera species across Iran (Figure 2; the results for each family are provided in Data S2). Here, the main bioregions refer to those detected geographic units that together cover more than 90% of the study area. Aside from the detected regions in the northwest and across the Alborz (Elburz) mountain range, there was a high degree of overlap between the bioregions identified by the two methods in the other areas when using the MCP + SDM approach (Table S3). Resulting bioregions by only occurrences were highly fragmented, with numerous units containing few cells in both CM and NM methods (Figure S5). While there was a higher overlap between detected units by NM using both MCP and MCP + SDM approaches, there was less consistency between the number and position of the units using CM (Appendix S1, Figure S7 & S9). Therefore, we here only compare the resulting units by CM and NM using species ranges by the MCP + SDM approach.

3.1 | Higher Species Richness Across the Mountain Ranges

As shown in Figure 3, the species richness for all examined families had a positive correlation with mountainous areas, mainly across the main mountain ranges of Alborz and Zagros (Figure 1). Although species of Lycaenidae (Pearson correlation coefficient (r) = 0.50)and Geometridae (r = 0.62) had a wider elevational distribution range, the richness of Zygaenidae species (r = 0.64) was restricted to higher elevation regions of the Alborz, Zagros and Ghohrud Mountains (Figure 3; Figure S6). Our results revealed a strong correlation between species richness and higher elevation and topological heterogeneity (Figure 3; see Data S2 for more details).

3.2 | Main Detected Bioregions

Here, we provide an overview of the main resulting bioregions from CM and NM according to the identified indicative species (the full results are provided in Table 2 and Data S2). For a better comparison between the resulting bioregions, we assigned a name to each according to the location of the bioregions (hereafter bioreg) of NM.

Alborz: One of the main differences between NM and CM is the bioreg2 in NM, which extends mainly from the southern Caucasus region in the northwest of Iran toward the northeast across the Alborz Mountains (Figure 2; Table S3). This bioregion has some overlap with bioreg2 and 5 of CM. However, none of the nine indicative species of bioreg2 by NM were the same as the indicative species of CM bioregions in the north and northwest (Table 2). Indicative species of bioreg2 of NM were shared with non-indicative species of bioreg1 of NM and bioreg1, 2, 5 and 6 of CM, e.g., *Cosmorhoe ocellata*, *Scotopteryx decolor* (Geometridae) and *Aricia vandarbani* (Lycaenidae; Table 2). This region encompasses 512 species, of which 83 species are endemic to the country (Figure 4a).

Zagros: Bioreg1 of NM extends from the northwest of the country toward the southwest and central regions across the Zagros Mountains (Figure 2). This bioregion is mainly comparable with bioregions 1 and 5 of the CM. Bioreg5 of CM in the northwest of Iran shared some species with bioreg1 of NM, e.g., endemic species of Lycaenidae (e.g., *Polyommatus luna*and *P. aereus*). Additionally, bioreg8 of NM in the very northwest on the border with Turkey had some identical species with bioreg5 of CM e.g., *P. myrrhinus and P. baytopi* and endemic species: *P. urmiaensis* (Lycaenidae) and *Rhodostrophia calabra* (Geometridae). Some endemic species, like *Zygaena mirzayansi* (Zygaenidae) and *Polyommatus peilei* (Lycaenidae) were indicative species for bioreg1 in both NM and CM methods. After the Alborz bioregion, the Zagros bioregion by NM has the highest number of species (319); of this number, 86 species are endemic in Iran (Figure 4a).

Central desert basins: Bioreg3 in NM and bioreg2 in CM are extended across the largest bioregions in Iran; some endemic species, such as *Plebejus ardashir*, *Polyommatus kermansis* (Lycaenidae) and *Rhodostrophia vahabzadehi* (Geometridae), were among the indicative species of these bioregions (Figure 2). The bioregion has 193 species, of which 61 are endemic for the country (Figure 4a).

Persian Gulf and the Oman Sea coasts: One of the distinctive bioregions in both methods was located across the northern seashores of the Persian Gulf and the Oman Sea (bioreg4 in NM and bioreg3 in CM). Bioreg4 in NM extended from the southwest of the country toward the southeast and shared a vast area with bioreg3 of CM (Figure 2). Endemic species, like *Scopula lactarioides* (Geometridae) and non-endemic species, such as *Azanus ubaldus*, *Anthene amarah* (Lycaenidae), *Isturgia disputaria* and *Microloxia indecretata* (Geometridae) were listed as indicative species by both methods (Table 2). This bioregion harbours 150 species of Lepidoptera, of which 27 species are endemic (Figure 4a).

Kopet-Dag: Bioreg5 of NM and bioreg4 of CM delineated a distinct bioregion across the Kopet-Dag Mountains in the northeast. Endemic species, like *Polyommatus tenhageni* (Lycaenidae), *Zygaenoprocris fredi*, *Z. khorassana* and *Zygaena esseni* (Zygaenidae), were among the most indicative species for both bioregions. Furthermore, some non-endemic species, such as *Cinglis eurata* (Geometridae), *Neolycaena tengstroemi*

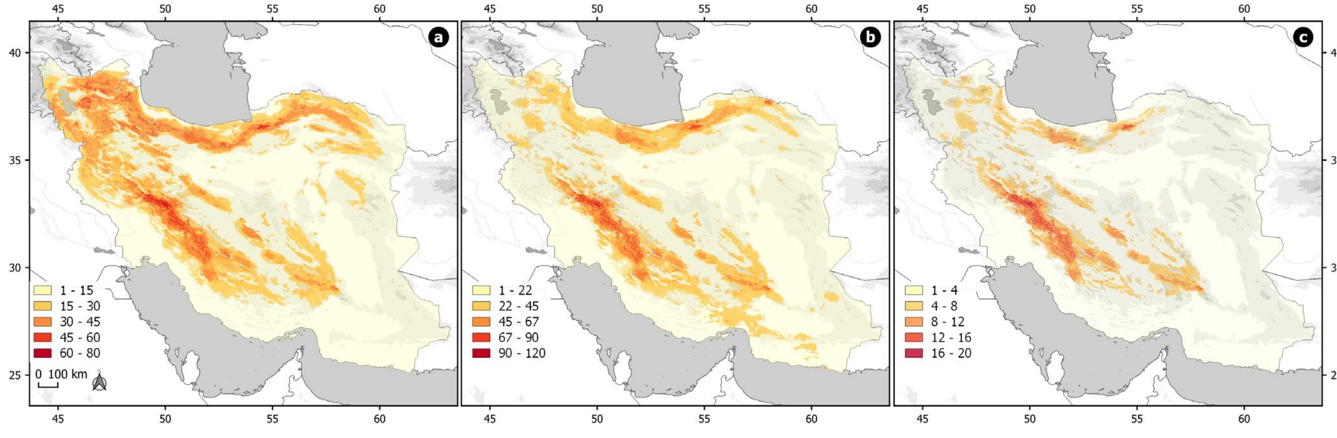

FIGURE 3 | Species richness of studied families based on the resulting species ranges by MCP + SDM: (a) Lycaenidae, (b) Geometridae, (c) Zygaenidae in Iran.

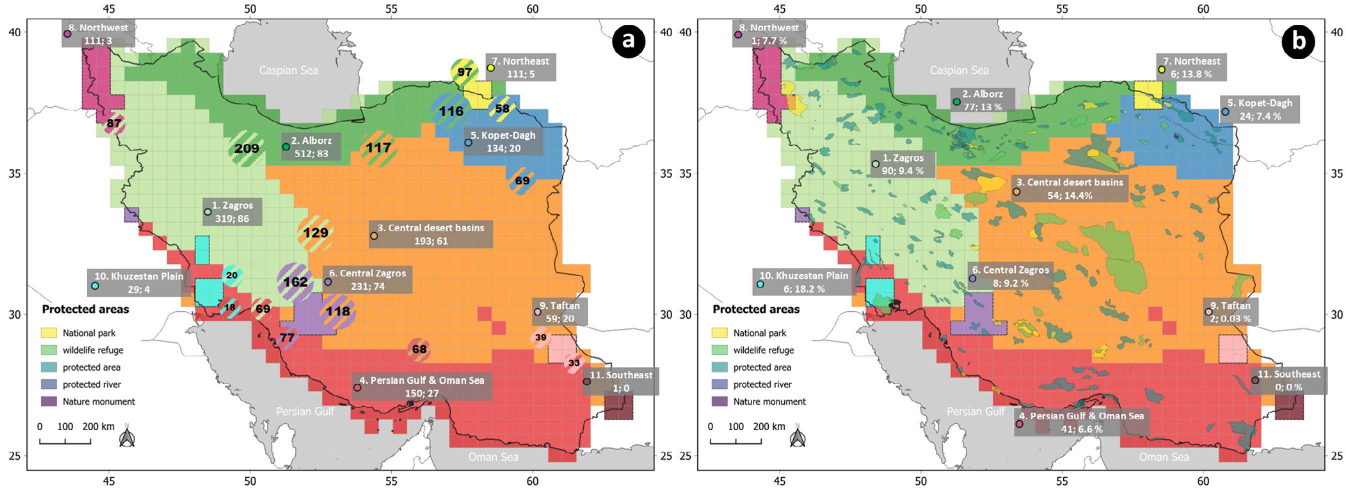

FIGURE 4 | The species composition and conservation of detected bioregion using network-based method in Iran. (a) number, name and species composition of each bioregion. The first number depict the species number and second one shows the number of endemic species. The circles and the number on the border of bioregions depict the number of shared species between different bioregions. (b) Distribution of different categories of protected areas (PAs) across detected bioregions. First number in the transparent rectangle show the number of PAs and second number is the coverage percentage of PAs across each bioregion.

(Lycaenidae) and *Zygaenoprocris albertii* (Zygaenidae), were indicative species of both bioregions (Figure 2, Table 2). In this NM bioregion, 134 species of Lepidoptera occurred, 20 of which are endemic (Figure 4a).

3.3 | Transition Zones

Besides the main bioregions, seven and six small regions each covering a few cells were detected in the overlapping areas of the main bioregions by CM and NM, respectively (Figure 2). These regions (zones) contained between two and 12 cells, mainly on the borders of the country with neighbouring countries. Zone6 and 7 from CM included some cells in the northeast and shared the most indicative species with zone7 of NM, e.g., *Stegania dalmataria*, *Phaselia narynaria* and *Protorhoe turkmenaria*, etc. (Geometridae; Table 2). Zone6 of NM represented a transition between three bioregions 1, 3 and 4 of NM (Figure 2b). The most indicative species for this bioregion were *Scopula hoerhammeri*, *Idaea wiltshirei* and *Eupithecia mahomedana* (Geometridae), which are shared with bioreg1 of CM. Despite its small size, this zone harbours 248 species. Zone10 of NM shared some indicative species with several bioregions of CM (e.g., *Phaiogramma polemia*, *Isturgia hopfferaria* with bioreg1, *Dicrognophos sartata* with bioreg1 and zone8 and *Pasiphila palaearctica* with bioreg3 (Table 2)). Moreover, there were some zones detected in the southeast: zone9 in CM and zone11 in NM (Figure 2). These zones were defined based on the two species *Tarucus alternatus* (Lycaenidae) and *Scopula ornata* (Geometridae) in NM and only by *Tarucus alternatus* in CM.

3.4 | Conservation Status of Lepidoptera Bioregions

We also assessed the coverage of PAs for the inferred bioregions. As shown in Table 3 and Figure 4b, for NM, while bioreg1 (Zagros) is covered by the highest number of PAs, this bioregion is covered by only 9.5% of its area. On the other hand, bioreg3 (Central desert basins) has the highest protection coverage with 14.6%, compared to the other identified bioregions. Bioreg2 (Alborz) is covered by 77 PAs, accounting for 13% of its area, while bioreg4 and bioreg5 have less than 8% of their area under protection. In the case of the potential transition zones, all zones—except Zone10 (Khuzestan Plain) which is covered by 6 PAs and 18.2% of its area—have less than 10% of their areas protected (Figure 4b). The lowest levels of protection are found in the two zones identified in the southeast of the country (Table 3). Almost similar results can be seen for bioregions as identified by CM (Figure S17 and Table S5; see Appendix S1).

4 | Discussion

This study aimed to investigate the biogeographic regions of Lepidoptera and their conservation status in Iran. Our analysis identified five major bioregions and two transition zones in the southern Central desert basins for Lepidoptera in the country based on the families Geometridae, Lycaenidae and Zygaenidae (Figure 2; Table 2; also see Data S2). Notably, we found that the most species-rich bioregions and potential transition zones are inadequately protected by the current network of protected areas (PAs) (Table 3; Figure 4b).

4.1 | Defining Species Ranges

Mapping the distribution of species' ranges accurately is crucial in conservation science, especially when systematic surveys are lacking (Woolley et al. 2020; Ginal et al. 2022; Hughes et al. 2024). In this study, we defined the ranges of species using three approaches to compare their effects on species composition of bioregions: (i) occurrences, (ii) MCP across suitable ecosystem patches and (iii) a combination of MCP with species distribution models (MCP+SDM; Doré et al. 2022; see Appendix S1). While bioregions defined by only occurrences are highly fragmented, there is a high overlap between detected bioregions by the MCP and MCP + SDM approaches, particularly for NM. Our results showed that MCPs can constrain the dispersal of species by excluding the edges of species distributions compared to MCP + SDM, while the use of SDMs provides more continuous and ecologically meaningful range estimates (Appendix S1; Figure S6 & S8; Hughes et al. 2024). This smoothing effect of using SDMs additionally to MCPs also contributes to delineating continuous bioregions, which can better estimate the ecological boundaries of the species (Paradinas et al. 2023). Although defining species ranges using SDM has been formerly criticised (Vilhena and Antonelli 2015), in line with previous studies, the results of this study revealed a good potential for the method to define species ranges based on the ad hoc data for defining bioregions and mapping species richness (Woolley et al. 2020; Doré et al. 2022; Hughes et al. 2024).

4.2 | High Species Richness Within Global Biodiversity Hotspots

Well-studied groups of Iranian Lepidoptera like Papilionoidea and Zygaenoidea show comparable diversity to the European fauna (Landry et al. 2023; Rajaei, Noori, et al. 2023). Iran hosts 469 species of Papilionoidea (Rajaei, Aarvik, et al. 2023), slightly more than 463 species found in the Mediterranean biodiversity hotspot (Numa et al. 2016), 17% and 21% of these being endemic respectively (Numa et al. 2016; Wiemers et al. 2018; Rajaei, Aarvik, et al. 2023). The rate of endemism for Papilionoidea in Iran increases across the mountainous areas (Noori, Hoffmann et al. 2023; Noori, Rödder, et al. 2024; Rajaei, Noori, et al. 2023). In line with previous research, we observed a strong correlation between endemism and species richness, and regions with higher elevation and topological heterogeneity in Iran (Figure 3; Data S2; Noroozi et al. 2018; Noori, Rödder, et al. 2024). Two out of the 36 global biodiversity hotspots extend across mountainous areas in the northern and western parts of the country (Mittermeier 2000; Myers et al. 2000). Similar patterns have been documented for a variety of fauna and flora as well (Noroozi et al. 2018; Noroozi et al. 2019; Yousefi et al. 2022). Globally, mountain ranges have been suggested as one of the main drivers for shaping species' distributions (Antonelli 2017; Ficetola et al. 2017). The mountain ranges in Iran provide a wide range of microhabitats, likely representing glacial refugia, and act as a barriers and corridors for the distribution of the fauna (Rajaei et al. 2013; Ghaedi et al. 2021; Yousefi et al. 2023).

4.3 | Bioregions in Iran

We found a clear subdivision of the Lepidoptera biodiversity within the country. We detected five major bioregions, most of which were largely supported by both clustering- (CM) and network-based (NM) methods (Figure 2; Appendix S1). Nonetheless, the outcomes of the NM were more consistent across the different species ranges of approaches tested, and it also suggested bioregions at finer resolution (Bloomfield et al. 2018). Previous studies reported higher sensitivity for the NM compared to the CM in detecting bioregions with clearer boundaries at finer resolution (Vilhena and Antonelli 2015; Bloomfield et al. 2018; Yusefi et al. 2019). One of the key strengths of NM is its ability to identify transition zones, which are detected through participation coefficient metrics, offering deeper insights into gradual changes in species composition across bioregions (Bloomfield et al. 2018). Furthermore, NM enables more comprehensive analyses of biogeographical relationships compared to simple measures, as e.g. used in CM, which are more sensitive to metrics, algorithms and data structures (Vilhena and Antonelli 2015; Bloomfield et al. 2018).

Detected bioregions by NM roughly align with the previous studies on the regionalization of Iran's fauna and flora (e.g., Blanford 1876; White and Léonard, 1991; Yusefi et al. 2019; Noori, Zahiri, et al. 2024; Figure 4). Most bioregionalization studies for the country were conducted using descriptive/qualitative approaches, with only a few studies employing clustering methods (Dubatolov and Zahiri 2005; Matov et al. 2008; Noori, Zahiri, et al. 2024). Yusefi et al. (2019) is the only comparable study that used both NM and CM to define bioregions of the mammals of Iran. While their results broadly align with our results, differences exist in the northern parts of Iran. For mammals, the areas across the Zagros, Alborz and Kopet-Dag Mountains were detected as only one distinct bioregion using NM (Yusefi et al. 2019), whereas we detected three distinct Lepidoptera bioregions. This might be explained by the higher diversity of Lepidoptera, the varying mobility of the studied species, and the fact that Lepidoptera tend to be more dependent on their habitats and host plants (Scoble 1995; Powell et al. 1998; Hofmann and Tremewan 2017). Furthermore, the major detected bioregions by NM in our study are largely consistent with the identified ecoregions (Dinerstein et al. 2017) and bioclimatic regions (Djamali et al. 2011) for the country (Table S3). Hence, it appeared that in comparison with CM, NM can better tackle the challenges in bioregionalization studies (Vilhena and Antonelli 2015; Yusefi et al. 2019).

4.3.1 | Affiliation of Bioregions

Most of the northern bioregions in Iran belong to the Palearctic realm. However, the species assemblages of the bioregions in the northwest of Iran primarily share species with the Caucasus, Transcaucasia, the north of Iraq and eastern Turkey (Hofmann and Tremewan 2017). The Alborz bioregion, as identified in our study, stretches from the northwest of the country to regions in the northeast through the Alborz Mountains (Figures 2 and 4). These Mountains act as a migration barrier between temperate bioclimates on the seashores of the Caspian Sea and the dry and hot areas of the central desert basins, at the intersection between the Euro-Siberian and Irano-Turanian phytogeographic regions (Figure 4; Table S4; Zohary 1973; White and Léonard, 1991; Djamali et al. 2011). For instance, species like *Zygaena araxis*, *Satyrium ilicis*, *Lycaena tityrus*, *Nychiodes waltheri* and *Hydria hyrcana*, etc., are distributed from Transcaucasia toward the western Alborz Mountains (Tshikolovets et al. 2014; Hofmann and Tremewan 2017; Wanke, Hausmann, Krogmann et al. 2020; Stadie et al. 2022). Additionally, some species like *Zygaena filipendulae*, *Z. purpuralis* (Zygaenidae); *Lycaena thetis, L. tityrus and Cupido minimus* (Lycaenidae) have their most southern and eastern distribution points across the Alborz Mountains or mountains of Azerbaijan in the northwest (Tshikolovets et al. 2014; Hofmann and Tremewan 2020a, 2020b).

Simultaneously, the Alborz Mountains act as a corridor connecting the Lepidoptera faunas of the Caucasus/Transcaucasia and Central Asia, e.g., *Lycaena phoenicurus*, *Satyrium spini*, *Callophrys rubi* (Lycaenidae), *Phaselia pithana* and *Lithostege excelsata* (Geometridae; Rajaei et al. 2011; Tshikolovets et al. 2014; Werner et al. 2023). For instance, several species like *Zygaena turkmenica* (Zygaenidae), *Nychiodes divergaria*, *Euphyia frustata*, *Philereme transversata*, *Hydria hyrcana* and *Rhodostrophia terrestraria* (Geometridae) are distributed from Turkey to Afghanistan through this mountain range (Rajaei 2012; Hausmann et al. 2016; Stadie and Stadie 2016; Stadie et al. 2022; Feizpour et al. 2018; Hofmann and Tremewan 2020a; Rajaei, Hausmann, Trusch, et al. 2022; Rajaei, Hausmann, Scoble, et al. 2022). The higher heterogeneity and the sharp change in climate across the Alborz Mountains partly explain the highest number of species and rate of endemism for Lepidoptera within this bioregion (Figure 4; Memariani 2020). Generally, the regions across the Alborz Mountains have been detected as a distinct bioregion for several taxa, e.g., tiger moths (Dubatolov and Zahiri 2005), ants (Paknia and Pfeiffer 2011), planthoppers (Mozaffarian 2013) and dragonflies (Schneider et al. 2018).

Similarly, the Kopet-Dag Mountains in the northeast of Iran serve as a barrier between the species assemblies of the Central desert basins and Central Asia fauna (Memariani 2020; Yousefi et al. 2023; Noori, Zahiri, et al. 2024) This region has already been suggested as a distinct bioregion for different taxa, including plants (Memariani 2020), lizards (Anderson 1968) and tiger-moths (Dubatolov and Zahiri 2005).

In terms of biodiversity, the Zagros bioregion identified in this study aligns with the western Irano-Turanian phytogeographical provinces (White and Léonard, 1991), and the Zagros woodlands for mammals (Blanford 1876). This bioregion is characterised by the presence of elements from the Transcaucasian and east Anatolian regions and a high rate of endemism for different taxa (Dubatolov and Zahiri 2005; Mozaffarian 2013; Hofmann and Tremewan 2017). Furthermore, some species of Lepidoptera are distributed in the southernmost extreme of their ranges to the central and southern parts of the Zagros Mountains, e.g., *Lycaena asabinus*, *Thomares calimachus* and *Ennomos quercaria* (Tshikolovets et al. 2014; Rajaei, Aarvik, et al. 2023).

The uplifting of the Zagros Mountains has been suggested as a crucial factor in the speciation and diversification of different taxa of vertebrates on the Iranian Plateau (e.g., Ahmadzadeh et al. 2017; Ghaedi et al. 2021; Yousefi et al. 2023; Noori, Zahiri, et al. 2024). This might partially explain the high number of species within this bioregion (319 species; Figure 4).

4.3.2 | Potential Contact Zones of Zoogeographic Realms

The largest bioregion is found within the Central desert basins (bioreg2 of CM and bioreg3 of NM), sharing the longest border and species with all other major bioregions (Figure 2a,b; Figure 4; Figure S17). By some differences, this region has been identified as a distinct bioregion for other taxa, e.g., mammals (Yusefi et al. 2019), lizards (Anderson 1968), ants (Paknia and Pfeiffer 2011) and tiger-moths (Dubatolov and Zahiri 2005). Theoretically, the Central desert basins and the southern parts of the Zagros bioregion are areas where the Palearctic meets the Saharo-Arabian region in Iran (Holt et al. 2013; Ficetola et al. 2017; Noori, Zahiri, et al. 2024). This intersection is evident in the Central Zagros (zone6) and the Khuzestan Plain (zone10 of NM), marked by a sudden shift from high elevation landscapes of the Zagros Mountains to lowlands in the north of the Persian Gulf (Figures 1 and 2). These two zones were also identified for the mammals of Iran as potential transition zones (Yusefi et al. 2019).

Besides the five major bioregions, we also detected small regions between the main bioregions by NM (zones Figure 2b; Table 2). Some of these zones, particularly on the border with neighbouring countries, might reflect misrepresentation because of the lack of entire species ranges. However, those detected zones within the country can be considered potential transition zones in the overlapping areas between the main bioregions (Figure 2b). Particularly, the high number of species in the Central Zagros (Zone6), combined with a high number of shared species with neighbouring regions, highlights this region's role as a transitional zone between the main detected bioregion (Figure 4). These zones meet the definition of a transition zone due to their position within overlapping bioregions, characterised by sharp environmental gradients and a noticeable replacement of characteristic species (Morrone 2004, 2023; Halffter and Morrone 2017). Therefore, small regions detected by the NM in the southwest of Iran, Zone6 (Central Zagros) and Zone10 (Khuzestan plain), probably represent contact zones of the Palearctic and Saharo-Arabian realms (Figures 2b and 4a; Table 2).

4.3.3 | A Corridor Between the Saharo-Arabian and Oriental Regions

Climatologically, the Khuzestan Plain and northern coastlines of the Persian Gulf and Oman Sea belong to the tropical macroclimatic region (Djamali et al. 2011). These regions have been suggested as a distinct ecoregion (Nubo-Sindiuan; Dinerstein et al. 2017; Figure 1), a bioregion for the flora (Saharo-Sindian; Zohary 1973; White and Léonard, 1991), and as a zoological subdivision for mammals (Mesopotamia and Persian Gulf shore; Blanford 1876), lizards (Anserson, 1986), ants (Paknia and Pfeiffer 2011) and planthoppers (Mozaffarian 2013). Species like *Anthene amarah* (Lycaenidae) with Saharo-Arabian affiliation are distributed from South Africa through the Arabian Peninsula to the northern seashores of the Persian Gulf. Additionally, Oriental species like *Tarucus nara*, *Lachides ella* (Lycaenidae), *Traminda mundissima* (Geometridae) and *Creatonotos gangis* (Erebidae) have the most western distribution in this region (Dubatolov and Zahiri 2005; Tshikolovets et al. 2014; Rajaei, Hausmann, Scoble, et al. 2022; Rajaei, Aarvik, et al. 2023). The northern seashores of the Persian Gulf and Oman Sea serve as concurrent pathways, connecting species with Saharo-Arabian affiliation from central Africa toward the northeast of Pakistan, India and Sri Lanka, e.g., *Argina astrea* (Erebidae), *Tarucus rosaceus*, *Azanus ubaldus* (Lycaenidae), *Traminda mundissima*, *Problepsis cinerea*, *Scopula adelpharia* and *Pseudosterrha paulula* (Geometridae; Dubatolov and Zahiri 2005; Tshikolovets et al. 2014; Hausmann et al. 2016; Stadie and Stadie 2016;

Feizpour et al. 2018; Rajaei, Hausmann, Scoble, et al. 2022). This is not limited to invertebrates, as in the case of mammals, the presence of Oriental elements such as the Asiatic black bear (*Ursus thibetanus*), the palm squirrel (*Funambulus pennanti*) and the Indian crested porcupine (*Hystrix indica*) has been documented at the southeastern-most corner of the country (Yusefi et al. 2019; Noori, Zahiri, et al. 2024).

5 | Conserving Bioregions for Lepidoptera

The overlap between Iran's current network of protected areas (PAs) and the Lepidoptera identified bioregions reveals a significant conservation gap, especially in regions with high endemism and diversity (Table 3; Figure 4a,b; Figure S17). While countries are committed to protect 17% of their land by 2020 and 30% by 2030 (Butchart et al. 2015; Farhadinia et al. 2022) according to the Aichi target 11 (https://www.cbd.int/sp/targets), the PAs in Iran cover only 11.24% of its land (Noori, Rödder, et al. 2024). Most large PAs are in the Central desert basins, likely designed for charismatic species like the Asiatic cheetah (*Acinonyx jubatus venaticus*), highlighting an uneven PA distribution (Figure 4). The Central desert basins bioregion hosts few, mostly non-endemic Lepidoptera species shared with neighbouring bioregions (Noori, Rödder, et al. 2024). Conversely, bioregions with higher species richness and endemism are poorly protected (Table 3). For instance, three major bioregions identified in this study, which align with two global biodiversity hotspots (Myers et al. 2000; Mittermeier 2000), have inadequate PA coverage: Alborz (13%), Zagros (9.5%) and Kopet-Dag (7.4; Table 3). Independent studies show that these areas host significant biodiversity (Noroozi et al. 2019; Yusefi et al. 2019; Noori, Rödder, et al. 2024), yet they lack proper protection for taxa such as mammals, reptiles and endemic plants (Farashi et al. 2017; Noroozi et al. 2019; Yusefi et al. 2019; Noori et al. 2021; Yousefi et al. 2023). This is concerning, especially since insects have historically been overlooked in the establishment of PAs globally (Dias-Silva et al. 2021; Chowdhury et al. 2022).

Currently, Iranian biodiversity faces significant anthropogenic pressure, specifically in northern and western regions (within global biodiversity hotspots; Karimi and Jones 2020) and is severely impacted by global warming and drought, especially in the southern regions (Segan et al. 2016; Vaghefi et al. 2019; Noori, Hoffmann, et al. 2023). Therefore, there is an urgent need to protect the unique species assemblages within bioregions and potential transition zones identified in this study.

6 | Conclusion

We here delineated bioregions for Lepidoptera in Iran which are largely in line with previously identified macroclimatic and phytogeographical regions (Figure 4). While these bioregions generally align with bioregions of vertebrates and other invertebrates, there are certain discrepancies which could potentially be attributed to differences in physiology and habitat preferences. This study, in line with previous studies, emphasises the crucial role of the country's mountains as barriers and corridors for shaping biodiversity patterns in southwest Asia. Future surveys and studies have the potential to reshape our understanding of the diversity patterns of Iranian Lepidoptera by uncovering new species, particularly in the less-explored regions of eastern and southern Iran. However, the main challenge of this study was the lack of data regarding the distribution of the targeted taxa in neighbouring countries. Although Lepidoptera Iranica provides a good dataset to generate a fine-scale resolution picture of these contact zones, delineating the borders of Iran as a macro-scaled transition zone would require a better understanding of the distribution of the families in the neighbouring countries. Considering the profound impacts of climate change in the Middle East and particularly southern regions of Iran, the bioregions and transition zones identified in the current study can provide guidelines to establish new PAs or upgrade the current PAs to protected areas with distinct evolutionary and ecological values.

Author Contributions

S.N. M.H. and H.R conceived the designed this study; S.N and. H.R. Data curation; S.N. and D. R. Data analyses and methodology; S.N., D.R., M.H., G.H.Y. and H.R. Writing original draft; S.N., D.R., G.H.Y., O.H., D.W., M.H. and H.R. Writing – review and editing

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The occurrences dataset used for the analyses is available in the Dryad data bank under the address: https://doi.org/10.5061/dryad.kwh70rzbz. The R codes used in this study are available online at: https://osf.io/dk8f6/?view_only=cf92bae6ad09429184482b385e4a0201. Additionally, environmental layers were derived from the public domain: https://chelsa-climate.org.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.